Viola perreniformis (L.G.Adams) R.J.Little & G.Leiper, *stat. nov.*, with notes on Australian species in *Viola* section *Erpetion* (Violaceae)

R. John Little[1] & Glenn Leiper[2]

Summary

Little, J. & Leiper, G. (2013). *Viola perreniformis* (L.G.Adams) R.J.Little & G.Leiper, *stat. nov.*, with notes on Australian species in *Viola* section *Erpetion* (Violaceae). *Austrobaileya* **9(1): 80–101.** *Viola perreniformis* (L.G.Adams) R.J.Little & G.Leiper is recognized as a distinct species in section *Erpetion* in Australia. A description of the species is presented. Leaf and floral characters of four closely related species in section *Erpetion*, *V. banksii* Thiele & Prober, *V. hederacea* Labill. subsp. *hederacea*, *V. perreniformis stat. nov.*, and *V. silicestris* Thiele & Prober, are compared and discussed. Various aspects of the biology of these species are discussed and provisional keys are presented based on floral and leaf characters. Comments are also provided for four other species in section *Erpetion*: *V. cleistogamoides* (L.G.Adams) Seppelt, *V. eminens* Thiele & Prober, *V. fuscoviolacea* (L.G.Adams) T.A.James, and *V. sieberiana* Sprengel, and a putative hybrid, *V. × zophodes* Thiele & Prober.

Key Words: Violaceae, *Viola*, *Viola* section *Erpetion*, *Viola banksii*, *Viola betonicifolia*, *Viola caleyana*, *Viola cleistogamoides*, *Viola eminens*, *Viola fuscoviolacea*, *Viola hederacea* subsp. *hederacea*, *Viola perreniformis*, *Viola sieberiana*, *Viola silicestris*, *Viola × zophodes*, anther gland, cleistogamy, nectary

[1]R. John Little, MagnaFlora, 16 Pebble River Circle, Sacramento, California 95831, U.S.A. Email: bugsandbunnies4u@sbcglobal.net

[2]Glenn Leiper, 30 Tweedvale Street, Beenleigh, Queensland 4207, Australia. Email: leiper30@bigpond.com

Introduction

Viola hederacea Labill. subsp. *perreniformis* L.G.Adams was one of eight subspecies recognized by Adams in the *V. hederacea* complex in Australia (Adams 1982a,b). This was the first attempt to classify the diversity of forms that had been assigned to *V. hederacea sensu lato* in section *Erpetion* (Sweet) Benth. & Hook.f. Later, James (1990) recognized seven forms (A through G) of *V. hederacea* in New South Wales based on leaf shape and pubescence, and in addition, elevated three of Adams' subspecies to species rank. Thiele & Prober (2003) summarized the taxonomic status of each subspecies of *V. hederacea* described by Adams with all subspecies except subsp. *perreniformis* and subsp. *curtisae* L.G.Adams having been elevated to species rank.

In the original description, *Viola hederacea* subsp. *perreniformis* was distinguished from *V. hederacea* subsp. *hederacea* by the erect, soft, short pubescence, by the corolla being more or less concolorous, pale (lazuline) blue-violet, with the anterior petal white at the base with violet-coloured veins, and distinguished from other *V. hederacea* subspecies by suborbicular leaves with a deeply cordate base (Adams 1982a). The epithet 'perreniformis' means 'very reniform.' Interestingly, the adjective 'reniform' with respect to leaves of subsp. *perreniformis* was not mentioned in the Latin diagnosis and appears only in the description of subspecies (Adams 1982b). The leaves of subsp. *hederacea* were stated by Adams (1982b) to be variable *but never suborbicular* (authors' emphasis). Adams reported that subsp. *perreniformis* occurred in coastal regions between Cairns, Queensland (Qld) and Sydney, New South Wales (NSW).

Some Australian botanists have considered *Viola hederacea* subsp. *perreniformis* as warranting specific status (e.g. Thiele & Prober 2003), but the nomenclatural change has not been made. Based on a study of the holotype and isotype as well as other collections of the *V. hederacea* complex at BRI, CANB, and NSW, and recent field observations by the authors, we believe subsp. *perreniformis* differs sufficiently from subsp. *hederacea* to warrant recognition at species rank, as *V. perreniformis*. The close relationship among the four taxa, *V. banksii*, *V. hederacea* subsp. *hederacea*, *V. perreniformis* and *V. silicestris*, can be seen in the morphology of their leaves and flowers.

Long regarded as a difficult taxon because of its many leaf forms, recent studies of the *Viola hederacea* complex in Australia in section *Erpetion* have begun to clarify relationships among taxa in this group. In 2003, Thiele & Prober presented the most comprehensive study and summary to date of species in section *Erpetion* (Thiele & Prober 2003), which included a circumscription of species in the *V. hederacea* complex, descriptions of several new species including *V. banksii*, and a key to most members of the complex. Their circumscription of *V. hederacea* did not include *V. hederacea* subsp. *perreniformis*, which they believed to be a taxon distinct from *V. hederacea*. Thiele & Prober (2006) described *V. silicestris* as a new species and discussed similarities and differences of it compared to four other species in section *Erpetion*: *V. cleistogamoides* (L.G.Adams) Seppelt, *V. fuscoviolacea* (L.G.Adams) T.A.James, *V. hederacea* and *V. sieberiana* Sprengel.

During our study of *Viola perreniformis*, we found that *V. banksii*, *V. hederacea* subsp. *hederacea*, and *V. silicestris* were the taxa most often confused with *V. perreniformis stat. nov.* In this paper we examine and compare these four species (collectively referred to herein as the "four taxa") with new and existing data, document previously unreported observations of various morphological features, and suggest topics for future study. The taxonomy of section *Erpetion* is challenging and far from complete. The four taxa and other species in the section appear to have many unique features not known to occur in other *Viola* species.

Materials and methods

In November and December 2011 and January 2012, the first author examined herbarium specimens in the *Viola hederacea* complex at the herbaria BRI and NSW, including specimens identified as subsp. *perreniformis*. Both authors conducted numerous field studies in Qld and NSW during this timeframe. In 2013, the first author continued study of species in the *V. hederacea* complex at the herbaria CANB and NSW, and both authors examined specimens at BRI identified as subsp. *perreniformis* and subsp. *hederacea*. Scanned images were examined of slides of the type of *V. hederacea* at CANB.

At BRI, all specimens previously determined as subsp. *perreniformis* were compared with the isotype housed at BRI and an image of the holotype housed at CANB. Specimens were then sorted into three groups: 1) specimens that matched or closely resembled the holotype and isotype (these specimens are listed below under *Additional specimens examined*); 2) specimens generally similar to the holotype and isotype, but with leaves too immature or in too poor a condition to make a definitive determination; and 3) specimens which, in the authors' opinion, did not fit the concept of the *perreniformis* taxon, most of which are referable to subsp. *hederacea*. Over 1000 high-resolution, digital photographs were taken of herbarium specimens to facilitate further study.

Field observations of *Viola perreniformis* were made by both authors in February 2013 at Nightcap National Park (NP) in NSW. The second author made additional observations and collections of this taxon in March, April, and May 2013 at Crows Nest NP and in March 2013 at Moogerah Peaks NP, both in Qld. In June 2013, the second author collected fresh flowers of *V. banksii* from Springbrook NP (possibly a horticultural escape) and Venman Bushland NP and *V. hederacea* from Springbrook NP, all sites in Qld; the anther

glands on these flowers were then observed with a stereozoom microscope. Using a stereozoom microscope with a camera attachment, the first author obtained micro-photographs of flowers and anther glands of *V. banksii* and seeds of *V. perreniformis* and *V. betonicifolia*.

The species description is based on a composite of observations and measurements of leaves, petioles, peduncles, and flowers from a) the holotype and isotype; b) from herbarium specimens at BRI, and c) from plants collected by the authors in 2012 and 2013 and photographs taken of fresh material. The number of 'crenations' (rounded lobes) on leaf margins were recorded only from one side of a leaf because on herbarium specimens, overlapping leaves often prevented observation of the entire margin.

As used herein in reference to pubescence, the term pilose means soft, thin, straight, and clearly separated hairs; the type of hairs on leaf surfaces of *Viola perreniformis*. Villous means ± densely covered with soft, thin, long, straight or sometimes shaggy hairs, not clearly separated; the type of hairs often found on petioles and peduncles of *V. perreniformis*.

Common abbreviations used in specimen citation include CP (Conservation Park), NP (National Park) and SF (State Forest).

Taxonomy

Viola perreniformis (L.G.Adams) R.J.Little & G.Leiper, **stat. nov.**; *Viola hederacea* Labill. subsp. *perreniformis* L.G.Adams, *Fl. Aust.* 8: 386 (1982). **Type:** Queensland. Port Curtis District: *c.* 40 km WSW of Gladstone, Many Peaks Range, 2 June 1977, *M.D. Crisp 2751 & R.K. Ellyard* (holo: CANB, image!; iso: BRI).

Plants perennial, often appearing acaulescent, 3–6.5 cm high, stoloniferous, rooted sections of the stolon forming rosettes of leaves on short, fleshy rhizomes. **Stems** sometimes present, 1–8 cm long. **Leaves:** stipules narrow-ovate or lanceolate, margin irregularly fimbriate, apex acute, long-aristate; petiole 9–23 cm long, sparsely or densely pilose or villous, occasionally glabrous; blade reniform, sub-reniform, or ovate (outline ovate, orbicular, suborbicular, or semicircular), 5.5–23 mm long, 7–27 mm wide, base cordate or deeply cordate, occasionally subtruncate or truncate, often with distinct sinus between lobes; margins ciliate or eciliate, uniformly or irregularly crenate from basal lobes to apex, 4–9(–10) lobes per side, sometimes poorly defined, occasionally some lobes ± serrate, apex acute, obtuse, or rounded, occasionally ± truncate, the midvein terminating in a blunt mucro; abaxial surfaces of mature and immature leaves sparsely or densely pilose, with hairs scattered on 1° and 2° veins or over entire surface, occasionally glabrous, small or immature leaves sometimes tomentose; adaxial surfaces of mature and immature leaves sparsely or densely pilose, with hairs scattered over entire surface, occasionally glabrous; blades bi-colored, darker green adaxially, lighter abaxially. **Flowers** solitary, peduncles arising from a fleshy, usually vertical rhizome, extending above the leaves, 25–77 mm long, sparsely or densely pilose or villous, occasionally glabrous; bracteoles narrowly linear or aciculate, 2.5–5 mm long, opposite or alternate, often above the middle during capsule development; sepals lanceolate, margin entire, scarious, eciliate, apex acute, usually gland-tipped, auricles not prominent, *c.* 0.5 mm long; upper petals erect in young and reflexed in mature flowers, pale blue-violet on both surfaces, white basally, occasionally with a faint or prominent violet-coloured blotch distal to the proximal white area; lateral petals spreading in new and twisted in mature flowers, pale blue-violet on both surfaces, occasionally appearing white distally, white basally with a green and white, ± 1–2 mm long, ± 1–2 mm wide indurate area at the base, often with a faint or prominent violet-coloured blotch distal to the proximal white area, with faint or prominent violet-coloured veins, usually with a dense patch of white clavate and cylindrical beards on proximal third of petal, often with some tips violet-coloured, distal beards sometimes entirely violet-coloured; lowest petal obovate to oblong, usually white on proximal half with a prominent green and white, 1–2 mm long, 1–2 mm wide indurate area at the base,

the distal half of petal pale blue-violet, the veins violet-coloured, prominent on adaxial surface, faint or prominent on abaxial surface, usually not extending to distal margin of petal, the midvein and the two adjacent veins distinct, prominent, parallel, ± same length, scarcely or not anastomosing (without evident, interconnecting 2° veins), 5–9 mm long, apex retuse, truncate, rounded, occasionally with a short, sharp or rounded point between two lobes, spur not present; style geniculate near attachment to ovary, ± terete, style head glabrous, not differentiated from style shaft; anthers cream-coloured, anther glands pale green, smooth, *c.* ½–2/3 as long as anther, prominent, margins of terminal anther appendages not hairy; pollen cream-coloured. **Capsules** 5–6 mm long, 3-valved, often purple-spotted, glabrous. **Seeds** ovoid, surface uneven to irregularly rugose, 1–1.2 mm long, shiny or dull dark brown mottled with patches of light brown or tan, elaiosome not present.

Additional selected specimens examined: **Queensland.** Cook District: Intersection of road to radio tower and Longlands Gap Road, Longlands Gap SF, Aug 2007, *Zich 617 & Quinn* (BRI, CANB). North Kennedy District: Mt Fox, Dec 1949, *Clemens s.n.* (BRI [AQ115414]). South Kennedy District: Dalrymple Heights & vicinity, Jul 1947, *Clemens s.n.* (BRI [AQ115415]). Leichhardt District: Carnarvon Creek Gorge, 70 miles [112 km] NW of Injune, May 1962, *Johnson 2411* (BRI); Blackdown Tableland, *c.* 1 km E of main N–S road crossing, Jan 1973, *Henderson H1392 & Sharpe* (BRI). Port Curtis District: *c.* 60 km SW of Gladstone, 8 km SE of Amys Peak, Jun 1977, *Crisp 2793* (BRI); Kroombit SF 316, Aug 1984, *Gibson 634* (BRI); Castletower Mt, Oct 1988, *Randall 591* (BRI); Portion 10 V, Oaky Creek, Castletower, Apr 1989, *Gibson TOI482* (BRI). Wide Bay District: Mt Woowonga, Woowonga Range SF, Jan 1982, *Forster PIF1153* (BRI); Tinana Creek at Missings Crossing, May 2001, *Stephens 138903A(11)* (BRI); Mt Boulder, SE of Gympie, Oct 1993, *Bean 6831* (BRI); Mapleton Logging Area, Mapleton SF, W of Mapleton, Mar 1998, *Bean 13121* (BRI, CANB, HO, MEL, NSW). Moreton District: Mt Mee SF 893, 2 km SE of Forestry office, Sep 1997, *Halford Q3357 & Boyle* (BRI); Alice Creek, 7.5 km ESE of Murphys Creek Rail Siding, Aug 1990, *Forster PIF7100 & Bird* (BRI); Mt Edwards NP, 14 km W of Boonah, Sep 1992, *Forster PIF11483 & Reilly* (BRI); Mt Edwards, Moogerah Peaks NP, *c.* 14 km W of Boonah, Feb 2010, *Halford Q9754* (BRI); Mt May, Sep 1992, *Forster PIF11794 et al.* (BRI); Southern slopes of Mt Greville, SW of Lake Moogerah, Jan 2007, *Phillips 1679 & Phillips* (BRI); Between N and S peaks of Mt Maroon, W of Rathdowney, Apr 2009, *Phillips 2006 & Phillips* (BRI); Cronins Creek between Mt Barney & Mt Ernest, Dec 1932, *White 8757* (BRI); Near summit of Mt. Lindsay [Lindesay], Sep 1973, *Dowling 109* (BRI). **New South Wales.** Terania Creek, 10 km NNE of The Shannon [Channon], Feb 1980, *Coveny 10628* (BRI); Summit of Mt Carnham, W of Grafton, in the Baryugil area, Jun 1993, *Bryant s.n.* (BRI [AQ566756]); Summit of Munningyundo Mt, Nymboida NP, between Grafton and Glen Innes, Mar 2003, *Bean 20105* (BRI); North Rocks Road, Nightcap Range, *Little 13697 & Leiper* (BRI).

Distribution and habitat: The species occurs in a series of disjunct localities from west of Cairns, north Qld, to Sydney in NSW. Recorded elevations of specimens examined in this study range from 75 m at Oaky Creek, Castletower to 1160 m at Mt Lindsay, both in Qld. Of the 14 specimens that provide elevation data nearly 60% were collected at 500 m or higher. Microhabitat situations reported by collectors include: moist situations in wet sclerophyll forests, in woodlands, in open eucalypt forests, on steep slopes, in crevices of rocky cliffs, cascading over rock faces with or without water flowing, on rhyolite or on rocky brown loam, granite, or sandstone; east, south, and west-facing slopes (**Fig. 1**).

Phenology: Flowering and fruiting occurs throughout the year.

Conservation status: *Viola perreniformis* is widespread, occurs in several National Parks, and is not known to be at risk.

Notes on *Viola* section *Erpetion*

Observations on aspects of morphological variation and reproductive biology focus primarily on the four taxa *Viola banksii*, *V. hederacea* subsp. *hederacea*, *V. perreniformis* and *V. silicestris*. Information is also presented for four other species in the section, *V. cleistogamoides*, *V. eminens* Thiele & Prober, *V. fuscoviolacea*, and *V. sieberiana* and a putative hybrid, *V. × zophodes* Thiele & Prober. Other taxa recognized in section *Erpetion* that are not discussed include *V. hederacea* subsp. *curtisiae* and *V. improcera* L.G.Adams.

Stolons and Rhizomes. All species in section *Erpetion* produce stolons and two small bracts are always present between stolon nodes. Thiele & Prober (2003) reported that
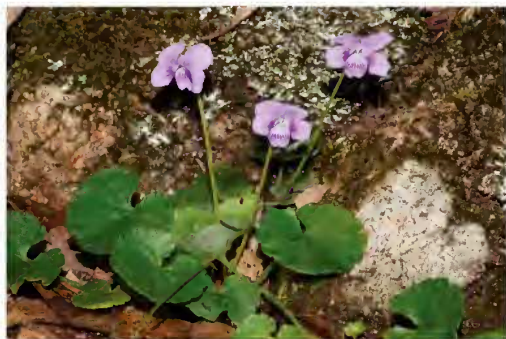
Fig. 1. *V. perreniformis*. Habitat, Crows Nest NP, Qld, Mar 2013. Photo: G. Leiper.

rootstocks of *Viola banksii* and *V. hederacea* were sometimes somewhat swollen and bulbous at the stem bases, but they were not or scarcely swollen in *V. silicestris* (Thiele & Prober 2006). The authors made similar observations for these species.

Stolons in section *Erpetion* are initially produced on the surface. Over time depending on their location, they can become buried with eroded soil, leaf litter, etc. Numerous herbarium specimens and the author's recent collections show that buried, subterranean stolons can eventually become lignified in some species. This phenomenon is not known to have been previously reported for Australian species of *Viola* in the section. Although a buried stolon is technically a 'rhizome,' buried stolons of these species do not become thick and fleshy, but retain their narrow shape.

A stolon node situated in a suitable site has the capacity to produce a vertically oriented rhizome and a rosette of leaves. As a rhizome matures it elongates vertically, its diameter increases, and it becomes fleshy, similar to many other *Viola* species. New leaves are produced distally as older leaves die. Leaf abscission scars and the remains of stipules are visible on the surface of the rhizome. If a vertically oriented rhizome is not buried, it can attain the appearance of a miniature tree; a large clone can attain the appearance of a miniature forest. A similar situation is sometimes observed in other *Viola* species e.g. *V. odorata* L. and *V. riviniana* Rchb. If a

vertically oriented rhizome is slowly buried with eroded soil, it can survive by elongating vertically, a useful strategy in a geologically unstable environment. All that may be visible at the surface is a rosette of leaves.

Although empirical data are lacking, it is possible that fleshy rhizomes function as water storage organs. Enlarged, subterranean rhizomes were found by the second author in a population of *Viola perreniformis* plants at Crows Nest NP, Qld (**Fig. 2**). Its gourd-like shape suggests it may function as a water and/or nutrient storage organ. Perhaps this rhizome was initially above ground and then subsequently buried; perhaps it was then able

Fig. 2. *V. perreniformis*. An enlarged, subterranean rhizome; length between arrows is *c.* 22 mm. Crows Nest NP, Qld, Mar 2013. Photo: G. Leiper.

to retain water more efficiently and gradually assumed a gourd-like shape.

Clones of some species can occupy up to 1 m or more in diameter. Although detailed studies of how these species spread via stolons have not been made, the first author recorded preliminary observations of the stages that a single 'mother' plant of *Viola hederacea* went through as it matured and spread over time; a brief description follows. After several leaves in the rosette of the mother plant matured and enlarged, five stolons developed that spread out in all directions. A rosette of miniature leaves formed at the distal end of each elongating stolon. If the stolon tip contacted suitably moist soil, a white, root-like structure developed and grew into the soil. After several days, the leaves in the newly rooted rosette increased in size and simultaneously

several new stolons formed and spread out in all directions and as they elongated, rosettes of miniature leaves formed at the tip of each new stolon. This process was repeated over and over in all directions from the initial mother plant until there was a mass of stolons and leaves *c.* 1 m in diameter. If a node didn't contact moist soil, the stolon continued to elongate, developing rosettes of leaves at each node. Because the available evidence suggests seeds of the four taxa may not be ant dispersed (see below) and they may not produce cleistogamous flowers (see below), vegetative reproduction through vigorous stolon growth may be an important strategy for survival in section *Erpetion*.

Stems. A valuable taxonomic character commonly used to separate *Viola* species in European, North American, and Asian floras, is whether the plant has stems (caulescent) or does not (acaulescent). Stems in caulescent *Viola* species are usually upright structures that originate from a fleshy or somewhat woody rhizome and possess alternating leaves subtended by stipules. Peduncles that produce chasmogamous and in many species, cleistogamous flowers, arise from axillary positions on the stem. In caulescent species in North America, the internode distance is usually short early in the growing season, elongating later in the season. Peduncles in caulescent species are normally produced only from stems and not directly from a rhizome. Caulescent *Viola* species in North America have both basal and cauline leaves, although a few species have only cauline leaves and no basal leaves. When present, basal leaves arise directly from the rhizome and are taxonomically useful in some species. In all *acaulescent* species known outside of Australia, the leaves and peduncles arise directly from a rhizome.

Of interest relative to the foregoing is that all Australian species in section *Erpetion* produce stolons. By analogy with the acaulescent, stoloniferous species in Europe and North America, species in section *Erpetion* would be assumed to be acaulescent. However, the *Viola* treatments in most Australian floras e.g. *Flora of*

Australia (Adams 1982b), *Flora of South-East Queensland* (Stanley & Ross 1983), *Flora of New South Wales* (James 1990), *Flora of Victoria* (Entwisle 1996), *Electronic Flora of South Australia* (2007), *Flora of Tasmania Online* (Duretto 2009), and *New South Wales Flora Online* (James 2013), state that stems are present for all species in the section. "Stems short" and "stems short, erect" are common descriptions in these floras for stems of species in section *Erpetion*. Also of interest is that the peduncles of all Australian species in section *Erpetion*, with two known exceptions, appear to develop only from rhizomes produced at a stolon node, similar to acaulescent, stoloniferous species elsewhere in the world. Thus, at present it appears that stems do not normally occur in section *Erpetion*, such as those typically found in caulescent species, e.g. *V. caleyana* Don in Australia.

A remarkable exception was documented by Thiele & Prober (2006) when they reported that *Viola silicestris* often develops "a caulescent growth habit when growing in sheltered sites amongst other vegetation, with elongate, weakly erect, scrambling aerial stems to 30 cm high and scattered leaves. Plants in exposed sites have contracted stems and fasciculate leaves". In northern NSW and Qld, we found stems on *V. silicestris* plants that had developed at stolon nodes and peduncles that developed from axillary nodes on the upright stems. Peduncles may also develop directly from rhizomes at stolon nodes, but this has not been verified. Stems can be short, e.g. 1.5 cm, or greatly elongated, 30–40 cm (Thiele & Prober 2006). The authors found a population in Springbrook NP, Qld, where clearly discernable stems occurred at 6 of 8 nodes on a stolon 75 cm long. At another location in Springbrook NP an 85 cm long stolon had discernable stems at 3 of 10 nodes. It may be that stem development in this species is more common, perhaps overlooked when stems are short and hidden in a rosette of leaves. The development of a *stem* from a *stolon* node has not previously been documented in other *Viola* species known to the authors and may be unique to section *Erpetion*. Acaulescent, stoloniferous species such as *V. odorata* typically root at a node and form a rosette

of leaves similar to the four taxa, but erect stems are never produced by such species at a stolon node. The growth habit of *V. silicestris* may represent a transitional stage from an acaulescent to a caulescent habit.

Viola perreniformis also produces stems. In 2013 the authors found plants with stems in Nightcap NP in NSW (*Little 13697 & Leiper* [BRI]) (**Fig. 3**). In addition, possible evidence of stems have been observed on several herbarium specimens at BRI that were collected in Qld and identified by the authors as *V. perreniformis*. Stems were not observed in populations of *V. perreniformis* at Crows Nest NP or on Mt Edwards (Moogerah Peaks NP) in Qld. Although phenotypically similar, it is possible these populations are genetically different and never produce stems, or stems were produced but overlooked, or perhaps microhabitat conditions precluded stem development.

Thiele & Prober (2006) noted that *Viola hederacea* and *V. sieberiana*, in contrast with *V. silicestris*, *never* (author's emphasis) develop a caulescent growth habit, even when growing amongst dense vegetation. Our observations of herbarium specimens and of living populations of *V. banksii* in Qld have not revealed evidence of stems. In *V. banksii*, *V. hederacea* and *V. sieberiana*, leaves and peduncles appear to arise only from a rhizome and never from a caulescent stem. These observations suggest these taxa could be acaulescent, although additional observations are needed. No data are available for *V. cleistogamoides* or *V. fuscoviolacea* regarding presence/absence of stems.

Leaves. The size and shape of leaves of most *Viola* species can vary greatly due to many factors, such as time of year (spring versus summer), the amount of soil moisture and other edaphic factors, and whether in sun or shade (Little & McKinney in press). Thiele & Prober (2006) appear to have been the first to document similar observations in reference to Australian violets, stating "This is a problem throughout the section, with reduced leaves of all species converging in shape [when immature] while fully developed leaves from sheltered sites are usually highly

Fig. 3. *V. perreniformis*. Pressed specimen showing stem (arrow) arising from a stolon node; 3 peduncles from the stem. Nightcap NP, NSW. Feb 2013. Photo: J. Little.

distinctive". They noted that most herbarium specimens fail to adequately represent the local variation present in leaves of species in section *Erpetion* and that the location of the plant, e.g. sun or shade, can have a profound effect on leaf size. We concur and emphasize that mature, fully developed leaves can facilitate identification of the four taxa. However, plants may have mature leaves that are not fully expressed, i.e. not typical, if they are growing in difficult sites (pers. comm., K. Thiele and observations by the authors). Thus, having fully developed, mature leaves may be essential for identification. In addition, it is necessary to consider all the leaves in a population and not focus on a few variants because in most populations of the four taxa, a few leaves can often be found at different stages of growth that are more typical of one of the other species. Also important to note is that various combinations of the four taxa are sympatric and it is possible that the stolons of two or more species could become intertwined in a given population resulting in some confusion if the leaves of one species

are associated with the flowers of another.

The leaves of all four taxa are darker green adaxially compared to lighter coloured abaxial surfaces (**Fig. 4**). The overall outline of *Viola banksii* and *V. perreniformis* leaves remain ± proportionally constant during development from immature to fully developed, whereas the leaves of *V. hederacea* and *V. silicestris* expand laterally as the blade matures, with the blade becoming much wider than long.

The information in **Table 1** is an attempt to qualitatively summarize and contrast morphological leaf characters in the four taxa typically found in fully developed leaves. Some characters for a given species

appear genetically fixed and do not vary, e.g. fully developed *Viola silicestris* leaves never have an orbicular outline; the outline of *V. banksii* and *V. perreniformis* leaves are never ± rectangular and their shapes are never falcate; a distinct sinus never occurs in fully developed *V. hederacea* or *V. silicestris* leaves, etc. As noted in the table, other morphological characters are only 'sometimes' present in a given leaf or population. 'Usually' in the table indicates the norm for the species, recognizing that variation occurs in that character. Immature leaves of some species have characters associated with fully developed leaves of other species (see discussions below).

Table 1. Qualitative summary of some leaf characters typically found in fully developed leaves of some *Viola* species

Leaf characters	*V. banksii*	*V. perreniformis*	*V. hederacea* subsp. *hederacea*	*V. silicestris*
outline orbicular	usually	sometimes	no	no
outline ovate	no	sometimes	no	no
outline ± rectangular	no	no	sometimes	sometimes
outline semi-circular	no	sometimes	usually	no
shape distinctly reniform	sometimes	usually	no	no
shape sub-reniform (i.e. cordate lobes not well developed)	no	sometimes	sometimes	sometimes
shape falcate	no	no	no	sometimes
leaf margins crenate <u>from base near petiole</u> to apex	no	usually	no	no[1]
leaf base cordate	yes	usually	no	no
leaf base truncate	no	sometimes	usually	usually
distinct basal lobes present	yes	usually	no	no
distinct sinus present formed by lobes	yes	usually	no	no
leaves much wider than long	no	no	yes	yes

[1]The distal leaf margins of *V. silicestris* are occasionally ± crenate, but the basal part of the blade is never crenate.

Viola banksii: Mature leaves ultimately attain an ± orbicular outline and shape or sometimes a reniform shape. The apex of mature leaves is usually truncate or rounded; a distinct mucro at the apex of the midvein is sometimes present; the base is cordate, never truncate. The two distinct basal lobes often overlap in fresh material, but overlapping lobes can be obscured when pressed. As the leaf matures and expands, the marginal teeth become further apart and often become small and less obvious on the upper half of the leaf. The margin is occasionally ± dentate. Occasionally small teeth and/or 3 or 4 small lobes (crenations) are present on the lower half of the leaf, but never around the entire margin. Mature, orbicular-shaped leaves are about as wide as long; reniform-shaped leaves are slightly wider than long. In small, immature leaves a distinct sinus is often present. A distinguishing characteristic of this species is the tendency for the apex of fully developed leaves to be truncate or somewhat rounded while also having cordate basal lobes and a distinct sinus (**Fig. 4**).

Viola hederacea subsp. *hederacea*: Mature leaves have been described as broad-reniform or semi-circular, usually truncate at the base and a margin with 8–16 teeth, the base occasionally with a broad sinus or broadly cuneate (Thiele & Prober 2003). Images of

Fig. 4. *V. banksii*. Sequence of development from new (1) to fully developed leaf (8). The smallest leaves often have a distinct sinus. Adaxial surfaces are shown; abaxial in 7. Pilose pubescence present on leaves and petioles. Photo: J. Little.

the type specimen show many small and large leaves with a distinct cuneate base. We found blade outlines of fully developed leaves to be ± rectangular (**Fig. 5.8**). Leaf apices are variable, rounded, obtuse, truncate, or occasionally convex. When the apex is truncate or convex, the outline is arguably not semi-circular, but closer to rectangular. The terminal midvein is usually just a small point or mucro. The distal (upper) leaf margin is ± entire with only a few short points where the major veins terminate. The base of fully developed leaves is usually

Fig. 5. *V. hederacea*. Sequence of development from new/immature (1) to fully developed leaf (8). Basal angle increases with age until becoming truncate in fully developed leaves. Adaxial surfaces shown. Photo: J. Little.

truncate and does not form distinct lobes as in *V. banksii* or *V. perreniformis*. Occasionally, the basal blade margin is curved or arched downward between the petiole attachment and the outermost edge of the blade, similar to *V. silicestris*. Such leaves are sometimes described as having a 'wide' sinus. The basal margin of young and fully developed leaves is entire or may have a small point or two and often forms a ± straight line between the petiole attachment and the outer edge of the blade. The angle formed by the leaf base in fully developed leaves is obtuse to usually truncate (180°).

Distinguishing features in fully developed leaves separating *Viola hederacea* (**Fig. 5.8**) from *V. banksii* and *V. perreniformis* are a truncate leaf base and lack of a sinus. Fully developed leaves of *V. hederacea* are somewhat similar to *V. silicestris* in that both can be ± rectangular and are much wider than long. Immature *V. hederacea* leaves usually have small lobes, but as the leaf matures and enlarges, the angle between the lobes gradually increases and the lobes 'disappear' as the base becomes truncate. Occasionally, small, immature leaves of *V. hederacea* have very distinct lobes and a distinct sinus and are very similar to immature leaves of other species, e.g. compare **Figs. 4.5, 5.3, 6.1**.

Our observations of herbarium and living specimens of *Viola hederacea* suggest that leaves that match the description of "broad-reniform" are not fully developed or perhaps were growing in difficult sites. The lobes in broad-reniform leaves are small (=sub-reniform) and the width of such blades are smaller compared to a fully developed leaf. The typical leaf shape of *V. eminens* was described as "broad-reniform" (Thiele & Prober 2003); however, we have not studied this species and our observations that broad-reniform leaves are not fully developed pertain only to *V. hederacea*. Although *V. hederacea* subsp. *hederacea* was reported to be replaced in Qld by *V. hederacea* subsp. *perreniformis* (Thiele & Prober 2003), many populations have been found in Qld that morphologically match the description of *V. hederacea* and are considered by the authors and others to be

V. hederacea. The second author has found several populations in Qld where the flowers are somewhat similar to *V. hederacea*, but the leaves are cordate or reniform with distinct basal lobes.

Viola perreniformis: Outlines of fully developed leaves are ovate, orbicular, suborbicular, or semicircular; their shapes are reniform or ovate. The apex is acute, obtuse, or rounded, occasionally ± truncate. The base of mature and immature leaves is usually cordate with a distinct sinus formed by the lobes of the blade. The sinus is usually distinct, but wider than in *V. banksii*. Most populations of *V. perreniformis* in Qld occasionally have some truncate and/or subtruncate leaf bases in addition to typical leaves with cordate bases, but these are usually associated with immature leaves. The marginal crenations (lobes) are usually quite uniform, but can be somewhat 'ragged' and irregularly shaped in some populations. Although the number of crenations per blade can vary in the same clone and among different populations, distinct crenations are present on most leaves in a clone. The number of crenations on one side varies from four in small/immature leaves to nine (seldom ten) in the largest/fully developed leaves. Fully developed leaves are usually slightly wider than long. Distinguishing features are leaves with crenate margins, usually around the entire blade in fully developed and usually also in immature leaves (**Fig. 6**).

Fig. 6. *V. perreniformis*. Sequence of development from immature (1) to fully developed leaf (5). Leaves at all growth stages are lobed. Adaxial surfaces shown. Photo: G. Leiper.

***Viola silicestris*:** Fully developed leaves have been described as broad, occasionally sub-reniform, the margin with (5–)7–12(–14) obscure teeth, the apical tooth not prominently larger than the rest (Thiele & Prober 2006). Here, we describe the overall outline of a fully developed blade as broad or ± rectangular, often with a falcate shape and occasionally sub-reniform. When falcate, the upper and lower margins are parallel. Occasionally a leaf is found with a shape resembling the tail of a diving whale. The apex is often truncate, sometimes rounded; the terminal midvein usually not much longer than the two adjacent veins, but sometimes shorter. The terminal midvein is usually just a small point or mucro. The blades are not distinctly lobed and a distinct sinus is not present. The base of fully developed leaves is truncate, although sometimes slightly curved or arched downward between the petiole attachment and the outermost edge of the blade. Occasionally, the blade bases curve upward from the petiole. The basal margin is entire or may have a small point or two. The distal leaf margin is ± serrate, subserrate, sometimes denticulate, or occasionally ± crenate. The outline of immature leaves is semi-circular or sub-reniform, smaller leaves are sometimes ± ovate; the apex obtuse or acute; the upper margin serrate, subserrate, or ± denticulate, the leaf base attenuate (cuneate) in some populations and truncate in others. Distinguishing features of this species are leaves that are usually much wider than long through all stages of growth from new/immature to fully developed. Fully developed leaves have a ± rectangular outline or falcate shape and never have distinct lobes or a sinus (**Fig. 7**).

Indumentum

***Viola banksii*:** This species was described as glabrous (Thiele & Prober 2003). However, several specimens at BRI collected in Qld have pilose hairs on adaxial, or on adaxial and abaxial leaf surfaces (e.g., BRI [AQ11278], [AQ115406]). A number of other populations in Qld appear to be *V. banksii* based on leaf shape, but the plants were variously pubescent on one or both surfaces, or leaves and petioles

Fig. 7. *V. silicestris.* Sequence of development from immature (1) to fully developed leaf (5). Leaves are much wider than long at all growth stages. Adaxial surfaces shown. Photo: G. Leiper.

were densely pubescent (**Table 2**). *V. banksii* plants are sold commercially worldwide under the name "*Viola hederacea*" (Thiele & Prober 2003; Elliot & Jones 2010). The first author has maintained a clone of *V. banksii* for over 10 years purchased as "*Viola hederacea*" from a nursery in Sacramento, California, U.S.A. The leaves, petioles, and peduncles on this clone are usually pubescent (**Fig. 4**), similar to some of the populations noted in **Table 2**. When leaves of *V. banksii* are pubescent, the margins are usually ciliate, as in *V. perreniformis*. Based on our observations of pubescence on *V. banksii*, we believe this character state needs to be recognized in descriptions of this taxon. Further study is needed of the populations noted in **Table 2**.

***Viola hederacea* subsp. *hederacea*:** Leaves were described as glabrous or with scattered unicellular hairs on the upper surface (Thiele & Prober 2003). Our observations of populations in southeast Qld and northern NSW are similar, although we have observed scattered hairs are sometimes present on both leaf surfaces. In addition, this species occasionally has hairs proximally on petioles and peduncles. In comparing the leaves of this taxon with *V. silicestris*, a general tenet is that *V. hederacea* leaves are often short-hairy, at least on adaxial surfaces, whereas *V. silicestris* leaves are usually glabrous.

***Viola perreniformis*:** Adams (1982b) stated that leaves of this species were softly pubescent, rarely almost glabrous. The authors

Table 2. Populations of pubescent *Viola banksii* cf. in Queensland

Location in Queensland	Comment
Pine Ridge CP and Jacobs Well (Gold Coast coastal areas)	Plants appear to be *V. banksii*. At both locations leaves have scattered hairs; at Jacobs Well, petioles are hairy.
Point Cartwright (Sunshine Coast)	Plants appear to be *V. banksii*. Leaves are sparsely hairy.
Alexandra Headland (Sunshine Coast)	Plants appear to be *V. banksii*. Leaves and petioles are very hairy.
Maroochy River CP (Sunshine Coast)	Plants appear to be *V. banksii*. Leaves with scattered hairs on both surfaces.
Ningi (Abbey Museum at the southern end of the Sunshine Coast)	Plants appear to be *V. banksii*. Leaves with scattered hairs on both surfaces.

conducted a brief evaluation of pubescence on leaf surfaces, petioles, and peduncles among *V. perreniformis* populations in Qld and NSW. The evaluation revealed substantial variation in pubescence on the same plant, between plants in the same population, and among different populations. Most populations were sparsely to densely pubescent on both leaf surfaces although the density of hairs usually varied between the abaxial and adaxial surfaces on the same leaf. Some populations had both glabrous and pubescent leaves on the same plant. Leaf margins were ciliate or eciliate. The petioles and peduncles of most populations were sparsely or densely villous, although some populations had both glabrous and pubescent petioles and peduncles on the same plant. No population was completely glabrous, although a population at Crows Nest NP in Qld was almost completely glabrous, with scattered pilose hairs only on the cordate lobes of the adaxial leaf surfaces. The pubescence on the abaxial surface of smaller leaves on the type specimens is considered tomentose, but larger leaves are considered densely pubescent. Based on our observations, we conclude the *absence* of hairs on leaves, petioles, and/or peduncles is not taxonomically useful. However, the *presence* of dense pubescence on leaves, petioles, and/or peduncles can be helpful for identifying *V. perreniformis* if appropriate leaf shapes and flower colours are also present. When leaves of *V. perreniformis* are pubescent, the margins are normally ciliate, as in *V. banksii*.

***Viola silicestris*:** Leaves of this species were described as glabrous or occasionally sparsely short-pubescent when young (Thiele & Prober 2006). Our observations of populations in southeast Qld and northern NSW are similar. The basal margins of young leaves on plants in Nightcap NP, NSW, occasionally had marginal cilia, but were otherwise glabrous. Many leaves on the isotype at BRI are ciliate (*Thiele 2568* [BRI]).

***Flowers. Petal movements and petal twisting*:** The two upper petals of the four taxa are sometimes described as "petals erect or reflexed". Reflexed upper petals and twisted lateral petals are common traits among the four taxa. Both authors have independently observed that petals of *Viola banksii* reorient themselves into a 'sleep' mode at dusk, then 'reopen' the next day. For example, as dusk approaches, the two completely reflexed upper petals of *V. banksii* flowers fold *forward* over the front of the flower (a movement of *c*. 180°) and the lateral petals 'untwist' and extend straight out in front of the flower. In the morning of the next day, the upper petals reflex *backward* (another *c*. 180°) from their forward position and the lateral petals spread back laterally to their normal daytime position and become twisted. Thus, the upper petals are 'erect' only for a brief period twice a day

Fig. 8. *V. perreniformis.* Erect upper petals; all petals pale blue-violet with violet-coloured blotches on upper and lateral petals. Moogerah Peaks NP, Qld. 2013. Photo: G. Leiper.

(Fig. 8), at least for the first few days after the flower first opens. Initial observations indicate that after several days, the petals no longer exhibit these nyctinastic movements. The first author and W. Cherry (pers. comm.) have independently observed nyctinastic petal movements in flowers of *V. silicestris*. This phenomenon is not known to have been previously documented in section *Erpetion* and its occurrence elsewhere in the section is unknown.

Flower colours: Flowers of *Viola perreniformis* and *V. silicestris* have been described as "concolorous" whereas flowers of *V. banksii* and *V. hederacea* have been described as "discolorous" (=bicoloured). Concolorous is also applied to the flowers of *V. cleistogamoides, V. fuscoviolacea* and *V. sieberiana*. The term concolorous in reference to the overall appearance of a flower is useful as an initial assessment to determine the species at hand, e.g., *V.*

perreniformis versus *V. silicestris*. However, because the face of *V. perreniformis* flowers often has darker coloured blotches on the upper and lateral petals, darker veins on the lowest and sometimes all petals, and because the petal bases are white, the description as 'concolorous' is sometimes not so clear cut.

The description of flower colours on collection labels can assist with taxon identification, but can be problematic for future researchers if ambiguous. For example, flower colours recorded for specimens we would consider *Viola perreniformis* based on leaf shape include the following descriptions: flowers pale blue; flowers purple; flowers sky blue; flowers violet with darker purple marks; flowers white and purple streaked; lilac-white flowers; mauve and white petals; violet flowers. None state whether the petal tips are white or not. Because the patterns of colouration on the face of flowers in the four taxa can be complex and because colours facilitate identification, we suggest 1) that names for flower colours, veins, and blotches be based on a readily available standard, and 2) that separate descriptions be recorded by the collector for the colour, presence or absence of darker coloured blotches, and presence or absence of darker coloured veins, for the upper and lateral petals, and for the lower (anterior) petal. For all petals, whether the tips are white or not should also be recorded.

The colours on petals of *Viola* flowers fade rather quickly on herbarium sheets and if not quickly pressed flat, the petals shrink and become distorted. These factors can make it difficult or impossible to determine the original colour scheme and/or petal shape on herbarium specimens. For example, within a month after collecting *V. perreniformis* and *V. silicestris* flowers, the distal portions of the petals, which had been pale blue when fresh, had faded in the press to a whitish colour.

Viola banksii and ***V. hederacea*** subsp. ***hederacea:*** Flowers of *V. banksii* were described as strongly discolorous violet-and-white (Thiele & Prober 2003). Flowers of *V. hederacea* were described as usually discolorous violet-and-white (occasionally concolorous pale violet or almost white),

the colours usually not strongly demarcated (*ibid.*). In general we concur with these descriptions, although some populations in Qld that appear to be *V. banksii* based on leaf shape have flowers that are not strongly demarcated and other populations that appear to be *V. hederacea* have flowers that appear to strongly demarcated. Among the possible explanations is that a greater range of variation needs to be recognized, or perhaps new taxa are involved.

Viola perreniformis: Adams noted that petal colours of *V. perreniformis* were pale (lazuline) blue-violet. We concur and have observed the abaxial surfaces of the five petals (**Fig. 9**) and portions of the adaxial surfaces (i.e., the 'face') are usually a pale blue-violet colour (**Figs. 8, 10**). The adaxial surfaces often have distinct purple blotches of various sizes on the lateral petals and occasionally basally on the upper petals (**Fig. 8**). In addition, faint to very distinct violet-coloured veins are often present on both surfaces of the lateral petals and lowest petal. The proximal portions on the adaxial surface of the upper and lateral petals are usually white, although it may be difficult to detect in some flowers without manually spreading the petals. The lowest petal is white proximally, blue-violet distally, and always has distinct, darker, violet-coloured veins (nectar guides). We observed substantial variation in the amount of pigmentation present on the 'face' of *V. perreniformis* flowers at Crows Nest NP, Moogerah Peaks NP and Nightcap NP.

Viola silicestris: Flowers were described as concolorous pale mauve-blue (rarely somewhat discolorous) (Thiele & Prober 2006), similar to our observations. At Springbrook NP, the authors found populations growing on rhyolite which had completely white flowers. These flowers did not have any darker coloured veins (i.e., no nectar guides) abaxially or adaxially on the upper, lateral, or lower petals.

Venation (nectar guides) on lowest petal: Venation of the lowest petal was determined to be a useful taxonomic character for distinguishing *V. banksii, V. hederacea,* and *V. silicestris* (Thiele & Prober 2003, 2006). We found general congruence with the venation

Fig. 9. Abaxial surface of *V. perreniformis* flowers wtih concolorous petals. Note the green and white indurate area at base of lowest petal (arrows). Crows Nest NP, Mar 2013. Photo: G. Leiper.

Fig. 10. *V. perreniformis*. Upper petals fully reflexed, lateral petals twisted. Crows Nest NP, May 2013. Photo: G. Leiper.

pattern described for these species in some populations, but not in others.

Green and white indurate area: A small, 1–2 mm long, 1–2 mm wide, green and white area is located at the proximal end of the lowest petal of the four taxa (**Figs. 9, 11**). A narrow, white, crescent-shaped zone usually occurs between the coloured part of the petal and the green area. A similar green and white area has been reported in *V. eminens* and is referred to as a "small green blotch" or "V-shaped blotch" in these species (Thiele & Prober 2003, 2006). *V. cleistogamoides* also has a green and white area on the lowest petal (Thiele & Prober 2006), but *V. fuscoviolacea* does not (Thiele & Prober 2003). No information is available for *V. sieberiana*. In addition to the colour being distinctly different from the rest of the petal,

Fig. 11. *V. banksii*, face view, lateral and upper petals removed. Yellow arrows point to anther glands. Green and white indurate area (not in focus) in lowest petal indicated by white arrow. Photo. J. Little.

we found the tissue in the green and white area in *V. banksii* and *V. perreniformis* flowers to be slightly 'harder' (indurate) compared to the rest of the petal, a feature not previously reported for flowers in section *Erpetion*. In flowers of *V. banksii*, *V. hederacea*, and *V. perreniformis*, we also observed a small green area at the base of the two lateral petals similar in colour to the indurate area on the lowest petal, a feature not previously reported in other species in section *Erpetion*. It has not been determined if the green area on the lateral petals is indurate compared to the rest of the petal. Although it may be presumed that the green and white indurate area in some way facilitates pollination and/or pollinator attraction, its purpose or function is unknown. When a flower is held up to a light source, the centre of the indurate area is translucent, perhaps functioning as a 'window' for the benefit of a pollinator. The lowest petal of most *Viola* flowers has the same texture throughout their length. For example, an indurate area at the base of the lowest petal was not reported for any of the 96 *Viola* species in China (Chen *et al.* 2008), nor any of the 73 *Viola* species in North America (Little & McKinney in press), and may be

unique to species in section *Erpetion*.

Style: The style of the four taxa is similar: a thin, straight, ± terete structure, except angled downward near the distal end toward the lowest petal; the style head is glabrous. The base of the style in the four taxa is geniculate near the attachment to the ovary, similar to many *Viola* species. The geniculate base facilitates the style shaft being easily moved when 'pushed aside' by insects probing for nectar or pollen. The geniculate portion of the style functions as a spring, allowing the style to be easily moved by the pollinator. After the pollinator withdraws, the style returns to its original position. In some *Viola* species in Europe, when the style is lifted up by a probing insect the anthers are spread apart and pollen is released (Beattie 1974).

Anther glands: The term 'anther gland', apparently first used by Thiele & Prober (2003), is an accurate and appropriate name for the glands found in the four taxa. Compared to the appendage and nectary found in many *Viola* species, the morphology and presentation of the anther glands in the four taxa are totally different. A few differences are highlighted. First, because the flowers have no spur, the anther glands are not protected within one; second, the anther glands develop laterally from and do not extend beyond the base of the anther; third, the nectaries in most *Viola* species are situated adjacent to each other whereas in the four taxa the anther glands are widely separated. In his description of the genus *Viola*, Adams (1982) stated that the anterior two anthers have "basal appendages" i.e., outgrowths from each anther, the distal portion of which secretes nectar. Although correct for species in which the two nectaries extend into a spur, e.g. *V. betonicifolia* and *V. caleyana*, it is inaccurate for the four taxa in section *Erpetion* because the anther glands are never longer than the anther and the nectaries are not enclosed in a spur.

When a flower is viewed face on with a hand lens, the two anther glands in flowers of the four taxa are seen 'hanging down' like landing gear on a plane (**Fig. 11, 12**). Remarkably, because the anther glands are not protected within the confines of a

spur, they are 'exposed' to the elements and potentially, it would seem, to physical damage from pollinators. Because the anther glands are situated above and immediately adjacent to the indurate portion of the lowest petal, one might assume that nectar would pool in the concavity formed by indurate area. However, we have not observed nectar in fresh flowers of the four taxa and are not aware of data demonstrating that nectar is produced in these species. In photographs of anther glands from freshly collected flowers of *Viola banksii*, *V. hederacea* and *V. perreniformis*, the glands were often 'glistening,' but obvious liquid nectar was not present. The lack of observations of nectar is not, of course, evidence that none is produced. Perhaps because they are not protected within a spur, the anther glands in section *Erpetion* have a different function other than to produce nectar. Pollen has been observed adhering to the anther glands in the four taxa presumably due to secretion of a viscid exudate.

The shape, colour, and surface texture of the anther gland is a useful diagnostic feature in section *Erpetion* (Thiele & Prober 2003). **Table 3** summarizes information for anther glands reported in the literature. **Table 4** summarizes preliminary observations made by the authors. The green colour of glands in some species is very similar to the colour of the indurate area of the lowest petal. The glands of some species are reported as pale or dull green or whitish. However, it is unknown if the colour is initially green and transitions to white or whitish over time, or vice-versa, or if some flowers typically produce only one colour, or if the gland is sometimes or always ± bi-coloured (e.g. white or pale distally, green proximally). A similar situation exists for gland surface texture. In a brief comparison of newer versus older flowers of *Viola banksii*, the first author found that glands of both newer and older flowers were white or whitish and both were rugose. However, the glands of this species have also been reported as pale green and smooth (**Tables 3 & 4; Fig. 12**).

The anther glands of *Viola silicestris* were described as "irregular, narrow" and an illustration shows them to be sinuous (Fig.
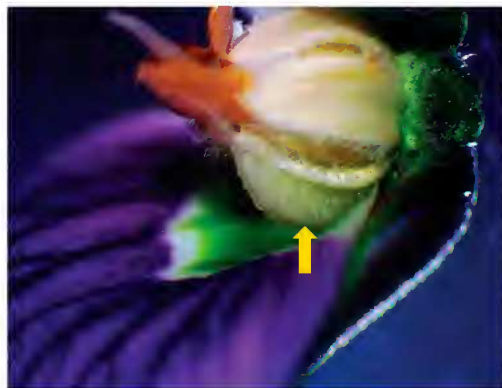

Fig. 12. *V. banksii*. Lateral view of one of the two anther glands (arrow). Lateral and upper petals removed. Photo: J. Little.

1 in Thiele & Prober 2006). However, in a population we sampled in Qld, the glands were prominent and curved, not narrow and sinuous. We believe that differences reported for shape, surface texture, and colour among the four taxa suggests that additional observations are needed. *V. hederacea* sometimes has purplish glands (Thiele & Prober 2003). A pure white flower of *V. silicestris* from Springbrook N.P. was found without an anther gland on either of the two lower anthers. A critical survey is needed of the morphology and development of anther glands, the role they play in reproductive biology, and a standard terminology developed for species in section *Erpetion*.

Pollination and cleistogamy. With certain exceptions, most species in the section have relatively large, showy flowers. Comparably sized flowers of *Viola* species in the northern hemisphere attract a wide range of insect pollinators such as solitary bees, bee-flies, syrphid flies and various Lepidoptera including butterflies and skippers. Beattie (1971) documented 43 different insect species in a *Viola* pollination study in England. The authors have not observed potential pollinators visiting flowers of any of the four taxa, although pollination of chasmogamous flowers is assumed to occur based on the many developing and dehisced capsules present in most populations and the fact that seeds are produced.

The fully reflexed upper petals of the four taxa could be an adaptation that facilitates sternotribic pollination by providing a platform on which insects can land. Sternotribic pollination occurs when an insect enters a flower 'upside down,' in contrast with nototribic pollination where the insect enters the flower in a supine position (i.e. 'right side up') (Beattie 1974).

Typical *Viola* pollinators seek nectar and/or pollen, although some are only after pollen. The authors have observed copious amounts of pollen in fresh flowers of each of the four taxa. A pollination study conducted with two *Viola* species in Brazil provided evidence that both species may be shifting from flowers that typically produce nectar, to flowers that provide primarily pollen (Freitas & Sazima 2003). The first author has observed yellow-coloured thrips (Thysanoptera) with pollen adhering to their bodies in *V. banksii* flowers, randomly and rapidly moving over and within dehisced anther sacs and around the ovary. Thrips were reported in *Viola* flowers (Baker 1935) and the first author has also observed them on flowers of several *Viola* species in California. Although thrips are often observed with pollen attached to them, there is currently no evidence they play a role in pollination of *Viola*. However, due to numerous observations of thrips in *Viola* flowers, it seems highly probable they could periodically affect pollination.

Cleistogamy occurs in many species of *Viola* throughout the world and is interpreted as a mechanism to help ensure survival when pollinators are unavailable. In North America, *c.* 85% of all species are known to produce cleistogamous (CL) flowers; only nine species are known to never produce CL flowers (Little & McKinney in press). In Asia, CL flowers are very common in most *Viola* species (J. Leng, pers. comm.). The presence or absence of CL flowers is not mentioned in Australian floras for any species of *Viola*. The authors have not observed CL flowers in the field or

Table 3. Summary of anther gland characters reported in the literature for *Viola*

Species/Source	Description	Surface Texture	Colour
V. banksii[1]	long, narrow and high, scarcely flattened	smooth	pale green to whitish
V. hederacea subsp. *hederacea*[1]	shorter than the anther cells, broad at the base and each distinctly flattened or depressed towards the other; short, rugose, often purple	irregularly rugose	purplish or dull green
V. silicestris[2]	slightly shorter than the anther cells, irregular, narrow	(Not reported)	pale

[1]Thiele & Prober 2003.

[2]Thiele & Prober 2006.

Table 4. Summary of anther gland characters recorded by authors

Species/Source	Description	Surface Texture	Colour
V. banksii Springbrook NP, Qld[1]	anther gland prominent, 'tall' or 'high', almost as long but not as wide as anther, wider proximally, slightly curved, 'top' of gland ± flat	smooth	pale green basally, ± greenish-white distally
Venman Bushland, NP, Qld	anther gland not prominent, short, *c.* ½ length of and not as wide as anther, gland height 'short', not 'tall' or 'high', appears ± 'flat' entire length of gland	smooth	white or whitish with a greenish tinge
Plant sold in U.S.A. as "*V. hederacea*"	anther gland prominent, 'tall' or 'high' almost as long but not as wide as anther, much wider proximally, curve, 'top' of gland ± flat	rugose	white or whitish or pale green entire length
V. hederacea subsp. *hederacea* Springbrook NP, Qld	anther gland prominent, almost as long and about as wide as the anther, gland is wider proximally, arched (curved), taller distally	at lower magnifications, the gland appears irregularly rugose; at higher magnifications the surface appears smooth; the uneven, rugose appearance appears to be caused by clumps of pollen grains adhering to the glandular exudate; the normally white pollen grains then take on a greenish colour	pale green basally, ± whitish distally; sometimes glistening when fresh
V. perreniformis	anther gland prominent, c. ½-⅔ as long as anther	smooth	pale green
V. silicestris Springbrook NP, Qld	anther gland prominent (on a violet-tinged anther), almost as long as, but narrower than the anther, proximal portion curved toward other gland	not determined	yellowish to pale

[1]Possibly a horticultural escape.

on herbarium specimens of the four taxa, nor on *V. sieberiana*. Cleistogamous flowers have not been observed on herbarium specimens of *V. cleistogamoides* or *V. fuscoviolacea* (the authors have not observed these species in the field). However, detecting CL flowers on herbarium specimens is difficult because CL flowers can appear similar to undeveloped or aborted chasmogamous flowers.

Viola species exhibit numerous strategies that promote reproductive fitness, one of which is hybridization that results in the formation of amphiploids, diploids, and tetraploids. As the authors have found and others have reported (Thiele & Prober 2006), some of the four taxa and other species in section *Erpetion* are sympatric. For example, in NSW sympatric populations occur with *V. perreniformis* and *V. silicestris*; *V. hederacea* and *V. silicestris*; and *V. fuscoviolacea*, *V. sieberiana* and *V. silicestris*; and in Qld, *V. hederacea* and *V. silicestris*. However, among the five species mentioned, no hybrids have yet been found (Thiele & Prober 2003, 2006). An example demonstrating that hybridization can potentially occur in section *Erpetion* was reported in Victoria between *V. eminens* and *V. fuscoviolacea* when an apparently sterile, but vegetatively vigorous putative hybrid, *V. × zophodes*, was found (Thiele & Prober 2003).

Adams (1982a) noted in the key to subspecies of *Viola hederacea* that subsp. *fuscoviolacea* L.G.Adams (=*V. fuscoviolacea*) was faintly scented. No other information on floral odours of species in section *Erpetion* is known to the authors.

Seeds and seed dispersal. Seeds of the four taxa, like most *Viola* species, have an ovoid outline, a shape that is assumed to facilitate ballistic travel after ejection from a capsule valve. The seeds of many *Viola* species possess an outgrowth, called an elaiosome or caruncle that develops around and extends out from the micropyle. Elaiosomes are fleshy food bodies of variable size that can be attractive to ants. Although the number of seeds examined in this study was limited, an obvious elaiosome was not detected on mature, recently collected seeds of three of the four taxa nor on *V. sieberiana* (seeds not

available for *V. banksii*). Seed characters reported in the literature and observed by the authors for the four taxa and *V. sieberiana* are summarized in **Table 5**. The seeds are small, 1–2 mm long, although *V. banksii* seeds are sometimes up to 2.5 mm long (Thiele & Prober 2003). While the first author was studying seeds of *V. sieberiana*, initial observations suggested that mature seeds were reddish-brown, until shiny black seeds were found. At least for this species, it appears that a reddish-brown colour transitions into black.

The apparent lack of an elaiosome in three of the four taxa and *Viola sieberiana* might lead one to suspect their seeds are not dispersed by ants. However, seeds of a *Viola* species in Europe with almost no elaiosome were reported to be removed by ants (Beattie & Lyons 1975). Lengyel *et al.* (2010) estimated that over 70% of Violaceae species throughout the world are myrmecochorous.

Based on numerous observations of dehisced capsules split into three valves on herbarium specimens and in the field, the dispersal mechanism of seeds from capsules in the four taxa and other species in section *Erpetion* is assumed to be similar to *V. betonicifolia* (Little & Leiper 2012). However, studies are needed to determine ballistic dispersal distances and to determine if ants play any role in dispersing seeds.

Taxonomic challenges

There is considerable evidence that *Viola* populations exhibit character divergence among local colonies of single species (Beattie 1976). It should therefore not be too surprising to find morphological variation among isolated populations of species in section *Erpetion*. Thiele & Prober (2003) noted there are several undescribed species in the *V. hederacea* complex in NSW. Recognition of new taxa may help resolve situations where observed character states in a population conflict with the current taxonomy of the complex. Additional study of the four taxa may reveal other morphological characters or relationships between characters that provide additional or better approaches for taxonomic

Table 5. Seed characters of five species in *Viola* section *Erpetion*

Species/ Location & Source	Mature Seed Colour	Surface Texture	Seed Length
V. banksii[1]	glossy purplish-black	± smooth to irregularly rugose	1.8–2.5 mm
V. hederacea subsp. *hederacea*[1]	dull, mottled cream and brown (occasionally uniformly reddish-brown)	± smooth	1.2–2.0 mm
Springbrook NP[2]	reddish-brown	warty-rugose	1.7–1.8 mm
V. perreniformis[2] Nightcap NP, NSW	shiny or dull dark brown mottled with patches of light brown or tan	uneven to irregularly rugose	1–1.2 mm
V. sieberiana[2]	shiny black	warty-rugose	1.5–1.8 mm
V. silicestris[3]	glossy purplish-black	not reported	1.5–1.7 mm
Springbrook NP[2]	shiny black	warty-rugose	1.6–1.7 mm

[1]Thiele & Prober 2003.

[2]Current authors.

[3]Thiele & Prober 2006.

recognition. Relationships in section *Erpetion* are largely unknown and will probably require DNA sequencing and chromosome counts to elucidate taxonomic relationships (Thiele & Prober 2006).

The provisional keys provided herein are based on the authors' observations and information in Thiele & Prober (2003, 2006). Among the four taxa, the flowers of *Viola perreniformis* are most similar to *V. silicestris*; flowers of *V. banksii* are most similar to *V. hederacea*. Fully mature leaves of *V. banksii* are in general more similar to *V. perreniformis*, whereas leaves of *V. hederacea* are in general more similar to *V. silicestris*.

**Provisional Key to selected species in *Viola* section *Erpetion*
(based on flowers and seeds)**

1 Abaxial surfaces of all petals usually of one colour (concolorous), entire surface pale violet, pale blue, or pale lavender, whitish or pale coloured proximally; on adaxial surface (face), *c.* half of upper and lateral petals pale violet or pale blue distally; (abaxial and adaxial surfaces of *V. silicestris* rarely mostly or entirely white); lowest petal obovate to oblong **2**

1. Abaxial surface of all petals usually of two colours (bi-coloured, or discolorous), petals white distally and pale violet proximally (*c.* 2/3 of upper petals white distally, pale violet proximally) on adaxial surface (face) *c.* 2/3 of upper petals white distally, violet proximally; *c.* half of lateral petals white distally, violet proximally; lowest petal obovate, elliptic, or circular **3**

2 Anthers cream-coloured; fully mature seeds shiny or dull dark brown,
　　1–1.2 mm long . . . . **V. perreniformis**
2. Anthers violet-tinged; fully mature seeds shiny black, 1.5–1.7 mm long . . . **V. silicestris**

3 Anther gland smooth or rugose, white or whitish to pale green; the
　　midvein and the two adjacent veins on lowest petal usually prominent and
　　distinct, often without interconnecting 2° veins; the violet and white areas
　　on petals usually strongly demarcated . . . . **V. banksii**
3. Anther gland usually rugose, dull green or purplish; the midvein on
　　lowest petal often less distinct than the two adjacent veins, often with
　　several to many 2° veins connecting them; the violet and white areas on
　　petals usually not strongly demarcated . . . . **V. hederacea**

Provisional Key to selected species in *Viola* section *Erpetion*
(based on mature, fully developed leaves)

1 Leaf base usually cordate, sinus and lobes usually present, sometimes
　　overlapping, blades about as wide as long (< 2× wider than long), blade
　　outline ovate, orbicular, suborbicular, or semi-circular, blade shape
　　orbicular, reniform, or ovate **2**
1. Leaf base usually truncate, sinus and lobes not present, blades usually
　　much wider than long (> 2× wider than long), blade outline
　　semi-circular or ± rectangular, blade shape broad-reniform or
　　sub-reniform (but lobes not prominent), or falcate (with the upper
　　and lower margins parallel) **3**

2 Leaf margin not crenate from basal lobes to apex, margin nearly entire,
　　sometimes ± scalloped or sinuous, outline usually orbicular, blade shape
　　orbicular or reniform, base cordate, lobes often overlapping in fresh
　　material, apex ± truncate, rounded or obtuse, occasionally ± dentate,
　　the midvein usually not extending much beyond the length of adjacent
　　veins, both leaf surfaces glabrous or with scattered, short hairs, never
　　tomentose, leaf blades about as wide as long . . . . **V. banksii**
2. Leaf margin regularly or irregularly crenate from basal lobes to apex,
　　outline ovate, orbicular, suborbicular, or semicircular, blade shape
　　reniform, sub-reniform, or ovate, base cordate, lobes seldom overlapping
　　in fresh material, apex usually acute, not truncate, midvein usually
　　extending beyond length of adjacent veins, both leaf surfaces often softly
　　hairy, occasionally tomentose, rarely sub-glabrous; leaf blades usually
　　slightly longer than wide . . . . **V. perreniformis**

3 The distal (upper) blade margin ± entire or with only a few short points;
　　stems not known to occur at stolon nodes . . . . **V. hederacea**
3. The distal (upper) blade margin ± serrate or subserrate, sometimes
　　denticulate, occasionally ± crenate; apex often truncate, sometimes
　　rounded; stems (1.5–40 cm) sometimes present at stolon nodes . . . . **V. silicestris**

Acknowledgements

References

ADAMS, L.G. (1982a). Appendix. Violaceae. In A.S. George (ed.), *Flora of Australia* 8: 386. Australian Government Publishing Service: Canberra.

ADAMS, L.G. (1982b). *Viola*. In A.S. George (ed.), *Flora of Australia* 8: 91–100. Australian Government Publishing Service: Canberra.

BAKER, M.S. (1935). Studies in western violets. I. *Madroño* 3: 51–57.

BEATTIE, A.J. (1971). Pollination mechanisms in *Viola*. *New Phytologist* 70: 343–360.

—— (1974). Floral evolution in *Viola*. *Annals of the Missouri Botanical Garden* 61: 781–783.

—— (1976). Plant dispersion, pollination and gene flow in *Viola*. *Oecologia* 25: 291–300.

BEATTIE, A.J. & LYONS, N. (1975). Seed dispersal in *Viola* (Violaceae): adaptations and strategies. *American Journal of Botany* 62: 714–722.

CHEN, Y., YANG, Q., OHBA, H. & NIKITIN, V. (2008). Violaceae. In *Flora of China* 13: 72–111. eFloras 2008. Published on the Internet http://www.efloras.org Missouri Botanical Garden: St. Louis, MO & Harvard University Herbaria: Cambridge, MA. Accessed 28 May 2013.

DURETTO, M.F. (2009). Violaceae. In M.F. Duretto (ed.), *Flora of Tasmania Online*. Tasmanian Herbarium, Tasmanian Museum & Art Gallery: Hobart. www.tmag.tas.gov.au/floratasmania. Accessed 28 May 2013.

ELECTRONIC FLORA OF SOUTH AUSTRALIA (2007). http://www.flora.sa.gov.au/cgi-bin/speciesfacts_display.cgi?form=speciesfacts&family=&genus=viola&species=&iname=&submit=Display Accessed 28 May 2013.

ELLIOT, R. & JONES, D. (2010). *Encyclopaedia of Australian plants suitable for cultivation* 9: 441. Lothian: Sydney.

ENTWISLE, T.J. (1996). Violaceae. In N.G. Walsh & T.J. Entwisle (eds.), *Flora of Victoria* 3: 361–370. Inkata Press: Melbourne.

FREITAS, L. & SAZIMA, M. (2003). Floral biology and pollination mechanisms in two *Viola* species – from nectar to pollen flowers? *Annals of Botany* 91: 311–317.

JAMES, T.A. (1990). Violaceae. In G.J. Harden (ed.), *Flora of New South Wales* 1: 435–441. Royal Botanic Garden: Sydney.

—— (2013). Family Violaceae, In PlantNET - The Plant Information Network System of The Royal Botanic Gardens and Domain Trust, Sydney, Australia (version 2.0). http://plantnet.rbgsyd.nsw.gov.au Accessed 28 May 2013.

LENGYEL S., GOVE, A.D., LATIMER, A.M., MAJER, J.D. & DUNN, R.R. (2010). Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: A global survey. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 43–55.

LITTLE, R.J. & LEIPER, G. (2012). Capsule dehiscence in *Viola betonicifolia* Sm. (Violaceae). *Austrobaileya* 8: 624–633.

LITTLE, R.J. & MCKINNEY, L.E. In press. Violaceae. In Flora of North America Editorial Committee (eds.), *Flora of North America North of Mexico*, Vol. 6. Flora of North America Association: New York & Oxford.

STANLEY, T.D. & ROSS, E.M. (1983). *Flora of South-eastern Queensland* 2: 99–101. Queensland Department of Primary Industries: Brisbane.

THIELE, K.R. & PROBER, S.M. (2003). New species and a new hybrid in the *Viola hederacea* species complex, with notes on *Viola hederacea* Labill. *Muelleria* 18: 7–26.

—— (2006). *Viola silicestris*, a new species in *Viola* section *Erpetion* from Australia. *Telopea* 11: 99–104.